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Peggy W. Lehman
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Interagency Ecological Program
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A Cooperative Program of:

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Executive Summary

A study of the tidal variation of phytoplankton biomass, cell diameter and species composition across the low salinity zone (the entrapment zone) and a qualitative evaluation of their possible influence on copepod food availability was conducted in spring 1994. The study found that the highest chlorophyll *a* concentrations, widest cell diameters and highest diatom densities occurred at the landward edge of the salinity zone in April and May and at the center of the zone in April. The lowest chlorophyll *a* concentrations and consistently high densities of *u*m diameter cells occurred at the seaward edge of the zone, where the green alga, *Nannochloris* spp., and the bluegreen alga, *Synechococcus* spp. were the most abundant phytoplankton.

Chlorophyll *a* concentration and large diatoms were not accumulated at the center of the low salinity zone by a gravitational circulation cell as was previously hypothesized. Hydrodynamic measurements indicated the salinity gradient was too small to produce gravitational circulation. Chlorophyll *a* concentration and cell diameter, however, accumulated with depth and tide at the center of the gradient. The highest biomass and nanoplankton density occurred on flood tide during the spring tidal cycle and total biomass was 2-3 times higher on both maximum ebb or flood tide. Among depths, chlorophyll *a* concentrations were 32% higher at the bottom and were associated with the presence of nanoplankton.

Near optimum predator/prey ratios, phytoplankton estimated spherical diameters, high chlorophyll *a* concentrations and high production rates of 10 *u*m diameter cells suggested the phytoplankton community provided good food quantity and quality for the most abundant copepods, *Eurytemora affinis, Sinocalanus doerii* and *Pseudodiaptomus forbesi* at the landward edge of the zone. The opposite was true at the seaward edge of the zone. Maxima of both phytoplankton and copepod biomass at the upstream edge of the low salinity zone, however, suggested most copepods had access to the high quantity and quality of phytoplankton food upstream. The major factor causing the low

chlorophyll *a* concentrations, small cell diameters and low diatom densities at the seaward edge of the zone was probably *Potamocorbula amurensis* grazing. As a result, management strategies to transport additional phytoplankton into the low salinity zone would probably not improve food availability for copepods at the downstream edge of the low salinity zone, because filtration by the clam would remove the additional phytoplankton and effect a reduction in cell diameter to below useable size.

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Abstract

Tidal day variation of phytoplankton chlorophyll *a* concentration, biovolume, cell diameter and species composition differed across the narrow, low salinity zone between 0.6 to 4 ppt and may influence copepod food availability in the San Francisco Bay Estuary. The highest chlorophyll *a* concentrations (range 3.2-12.3 $\mu g\ l^{-1}$), diatom densities and production rates of >10 µm diameter cells and widest cell diameters (>5 µm diameter) occurred at the landward edge of the salinity zone in both April and May. Near optimum predator/prey ratios, prey estimated spherical diameters and high chlorophyll *a* concentrations suggest these phytoplankton communities provided good food quantity and quality for the most abundant copepods, *Eurytemora affinis*, *Sinocalanus doerii* and *Pseudodiaptomus forbesi*. At the center of the zone, chlorophyll *a* concentrations and diatom densities and production rates of >10 µm diameter cells were lower and cell diameters were smaller than upstream. Downstream advection at the center of the zone was reduced by accumulation of phytoplankton with depth and tide; maximum chlorophyll *a* concentrations occurred during spring flood. The lowest chlorophyll *a* concentrations (1.4-3.6 $\mu g\ l^{-1}$) and consistently high densities (3000-4000 cells ml^{-1}) of <5 µm diameter cells occurred at the seaward edge of the zone, where the green alga, *Nannochloris* spp., and the bluegreen alga *Synechococcus* spp. were the most abundant phytoplankton. Low chlorophyll *a* concentrations, small prey estimated spherical diameter, low production rates of >10 µm diameter cells and high predator/prey ratios suggested the seaward edge of the zone had poor food for copepodids and adult copepods. Decreased phytoplankton chlorophyll *a* concentration, species composition and cell diameter across the low salinity zone was probably a function of both increased clam herbivory since the mid-1980s and decreased chlorophyll *a* concentration, cell diameter and diatom density since the early 1980s.

Introduction

High chlorophyll *a* concentrations and densities of large diatoms in the low salinity zone (LSZ) between 0.6 and 4 ppt were considered important for estuarine food web production in San Francisco Bay Estuary (SFBE) (Arthur and Ball 1979). A Suisun Bay location of the LSZ during spring in the 1970s coincided with high chlorophyll *a* concentration and densities of large diatoms, like *Skeletonema costatum*, *Coscinodiscus* spp. and *Cyclotella* spp., at the center of the zone (Arthur and Ball 1979; Ball and Arthur 1979; Cloern 1979; Wong and Cloern 1981; Cloern et al. 1983). High chlorophyll *a* concentrations at the center of the zone were hypothesized to be a function of accumulation by a gravitational circulation cell (Peterson et al. 1975; Arthur and Ball 1979; Cloern et al. 1983) and aggregation of <10 μm diameter freshwater phytoplankton cells exposed to brackish water (Arthur and Ball 1979; Ball and Arthur 1979).

Accumulation of phytoplankton biomass in the LSZ was considered to be a primary factor controlling the interannual variation of fish populations that use Suisun Bay, because it supported zooplankton production needed for larvae (Arthur and Ball 1979). The link between production in Suisun Bay and fishery resources was supported by statistical analyses which demonstrated a density maximum for many organisms in the food web when the center of the LSZ (2 ppt) was located in Suisun Bay (Jassby et al. 1995) and correlation between chlorophyll *a* concentration and zooplankton density (Orsi and Mecum 1996; Kimmerer and Orsi 1996; Kimmerer et al. 1994) or biomass (Lehman 1992).

Decreased chlorophyll *a* concentration and shifts in species composition since the early 1980s throughout the estuary (Lehman and Smith 1991; Lehman 1992, 1996a) and the factor of 10 decrease in chlorophyll *a* concentration in Suisun Bay since 1986, associated with the introduction of the Asian clam *Potamocorbula amurensis* (Nichols et al. 1990; Alpine and Cloern 1992), have raised questions on the ability of the current phytoplankton production in the LSZ to support zooplankton production. Phytoplankton biomass and species composition in the LSZ should still be important for zooplankton in the Suisun Bay region, because alternate food sources are few. Bacteria have higher rates of production than phytoplankton in the estuary (Werner and Hollibaugh 1993), but are not more abundant in the LSZ than upstream during the spring (J. T. Hollibaugh, personal communica-

tion). Rotifers (Obrebski et al. 1992) and other microzooplankton that commonly link the bacterial food source to the macro-and meso-zooplankton are not abundant (J. T. Hollibaugh, personal communication) and have decreased over time (Obrebski et al. 1992). Chlorophyll *a* concentration can reach pre-clam levels in wet years (Lehman 1996b) and diatoms are still the primary food found in the gut of copepods (Orsi 1995). The spatial and temporal contribution of phytoplankton to organic matter transfer in the food web is unknown.

Research in other estuaries has demonstrated strong spatial and temporal variation in phytoplankton biomass, species composition and cell diameter across a narrow salinity zone like that in SFBE. Longitudinal gradients often characterize chlorophyll *a* concentrations in rivers, where downstream concentrations increase on ebb tide, when advection transports phytoplankton downstream (Malone 1977; La Fleur 1979; Demers et al. 1986; Dustan and Pickney 1989); and during neap tide, when advection of upstream phytoplankton is high and mixing is reduced (Sinclair 1978; La Fleur 1979; Seliger 1981; Le Fevre 1986; Frenette et al. 1995). In fact, chlorophyll *a* concentrations were higher on ebb tide in South San Francisco Bay (Cloern et al. 1989). Frontal zones created by the convergence of seaward river flow and landward tidal flow can also concentrate phytoplankton biomass at the center of the salinity gradient in rivers (Dustan and Pickney 1989) and along the coast (Le Fevre 1986).

In a similar fashion, species composition varies along the longitudinal axis of estuaries in response to advection and mixing associated with ebb-flood asymmetry and causes an increase in freshwater species downstream on ebb tide (Sinclair et al. 1978; La Fleur 1979; Frenette et al. 1995). Changes in species composition caused by advection (Sinclair 1978; La Fleur 1979; Sinclair et al. 1980; Frenette et al. 1995) and mixing (Levasseur et al. 1984; Demers et al. 1986; Turpin and Harrison 1980) also influence the size structure of the phytoplankton community along the gradient. In addition, sedimentation and resuspension create vertical structure along a salinity gradient by increasing biomass and large diameter cells near the bottom (Frenette et al. 1995), where they may be trapped by horizontal salinity shear (Therriault et al. 1990).

The purpose of this study is to: (1) characterize the intertidal spatial and temporal variation of chlorophyll *a* concentration, phytoplankton cell diameter and species composition in the 0.6-4 ppt LSZ during the spring, (2) determine if the characteristics of the phy-

toplankton community in the LSZ have changed over time, and (3) qualitatively assess the current potential of the phytoplankton biomass, cell diameter and species composition to meet the expected quantity and quality of food needed by copepods in the LSZ. This information can assist evaluation of the current estuarine management strategies that position the LSZ in Suisun Bay during the spring and is a first step in evaluating the importance of phytoplankton food quantity and quality to zooplankton production in the estuary.

Methods

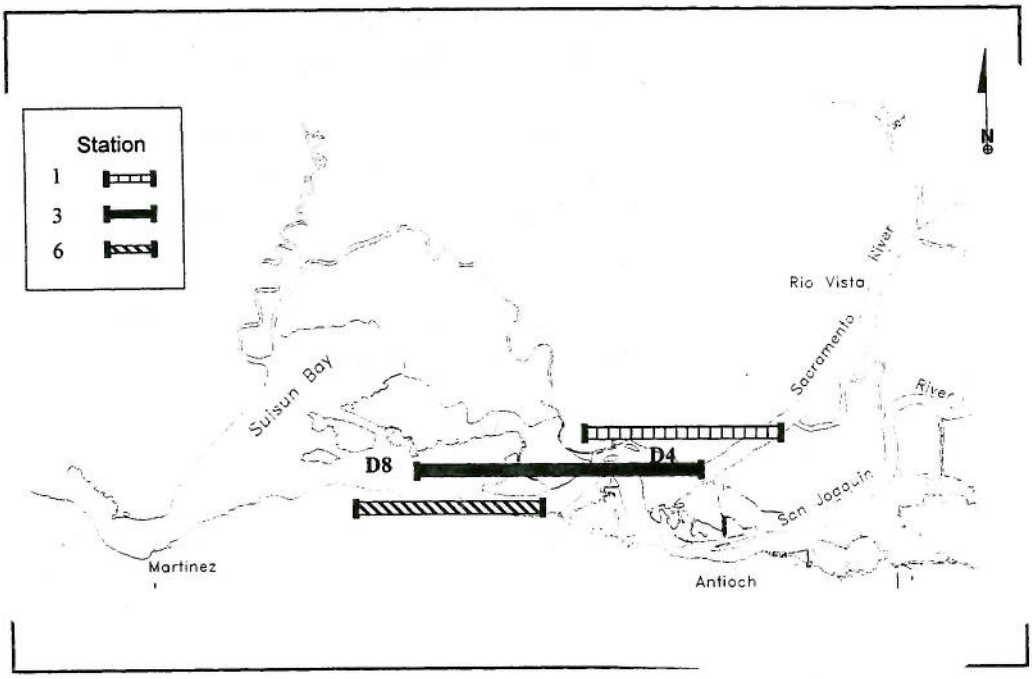
Phytoplankton and zooplankton were collected at 1, 5, and 10-m depths for a full tidal cycle (30 hr) during a strong spring tide on April 27-28, 1994, and a strong neap tide on May 17-18, 1994. Water samples for phytoplankton and zooplankton were collected using a submersible pump as the sampling boat moved from 1 to 3 and then to 6 m $Sm.^{-1}$ (hereafter stations 1, 3 and 6, respectively) and back again (Figure 1). Specific conductance values are equivalent to salinities of 0.6, 2 and 4 pp, based on salinity conversion equations that include corrections for water-year type and location (California Department of Water Resources DWR). This Lagrangian sampling scheme enabled samples to be collected at ebb, flood and slack tide at station 3 and at ebb and flood tide at stations 1 and 6. More samples were collected at the 2-ppt station, because it is hypothesized to be an important location for aquatic production in the San Francisco Bay estuary. Additional samples collected along the longitudinal axis of the estuary by a second boat, provided information on the phytoplankton communities upstream and downstream of the LSZ.

Replicate water samples for chlorophyll *a* measurement were filtered onto 0.4 μm pore size GF/C glass fiber filters, which were neutralized with magnesium carbonate and frozen until analysis.. Chlorophyll *a* was extracted using a mixture of acetone, dimethyl sulfoxide (DMSO) and water in a ratio of 9:9:2 and concentrations were calculated from fluorescence on a Turner Designs model 10 fluorometer using equations derived from Strickland and Parsons (1972). Total chlorophyll *a* concentration was measured at all stations. In addition, chlorophyll *a* concentrations in ultraplankton (< 5 μm), nanoplankton (5-20 μm) and microplankton (> 20 μm) size fractions were measured at station 3. Chlorophyll *a* concentrations in the < 5 μm and < 20 μm

size fractions were determined from filtrate collected after passing the water sample through a 5 or 20 μm nitex sieve. Concentrations in the 5-20 μm and >20 μm size fractions were determined by subtraction.

Water samples for phytoplankton analysis were placed in 50-ml glass bottles and preserved with Lugol's solution. Phytoplankton species composition, density and cell dimensions were determined from settled samples (Utermohl 1958) in which all of the cells on the bottom of the settling chamber visible at 1250X magnification were counted. Phytoplankton were categorized as microplankton, nanoplankton or ultraplankton, using cell diameters and the same size categories used for chlorophyll *a* size fractions. Phytoplankton species were grouped according to Lehman (1996a). Biovolumes were calculated using measured cell dimensions applied to simple geometrical shapes and corrected for the large vacuole in diatoms (Strathmann 1967).

FIGURE 1. Map of Sampling Area and Sampling Stations near Suisun Bay.



Zooplankton water samples were passed from the submersible pump (100 l min^{-1}) through a non-collapsible hose into a 30 cm diameter zooplankton net (35 mesh). Zooplankton collected in the cod end of the net were immediately preserved in 2-5% formalin and were sorted and identified to species using a dissecting microscope.

The optimum size phytoplankton food for copepods was estimated using equivalent spherical diameters (ESD) for phytoplankton and predator to prey ratios which were calculated as the ESD for copepods divided by the ESD for phytoplankton cells collected simultaneously (Hansen et al. 1994). Estimated spherical diameters were determined for phytoplankton from biovolumes and for copepods from dry weight conversions to volume using the equations of McCauley (1984). Copepopd dry weights for each species were obtained from J. Orsi, California Department of Fish and Game (DFG) (unpublished data)

Phytoplankton and zooplankton production rates were estimated from calculated values. The phytoplankton production rate of >10 μm diameter cells was calculated using estimates of cell carbon based on corrected biovolume (Strathmann 1967) and a carbon to chlorophyll ratio of 50 (Jassby and Powell 1994). Zooplankton production rate was calculated using estimates of carbon (Hansen et al. 1994) from dry weight and a copepod growth rate of 0.10 day^{-1} for adults and 0.27 day^{-1} for juveniles (Peterson et al. 1991).

Tidal velocities were measured at each station using an acoustic Doppler Continuous Profiler (ADCP) attached to the side of the ship. Velocities (cm s^{-1}) were measured at 0.25-m intervals from the bottom and averaged over the depths at which samples were taken.

Long-term monitoring data used for comparison with the data in this study were obtained from the Interagency Ecological Program data files of the California Department of Water Resources (DWR), U. S. Bureau of Reclamation (USBR) and DFG.

Nonparametric statistics were used to analyze most of the data and included single (chi square) and multiple (Kruskal-Wallis) comparison tests, correlation (Spearman) and linear trend analyses (Kendall Tau b).

Results

Phytoplankton Biomass

Phytoplankton biomass decreased seaward across the LSZ in both April and May. Median chlorophyll *a* concentration decreased from 4.5-9 $\mu g\ l^{-1}$ at station 1 (range 3.2-12.3 $\mu g\ l^{-1}$) to 2.4-2.5 $\mu g\ l^{-1}$ (range 1.45-3.6 $\mu g\ l^{-1}$) at station 6 (Figure 2). This decrease was part of a larger-scale decrease in chlorophyll *a* concentration along the longitudinal axis of the estuary, from a peak concentration of 12-17 $\mu g\ l^{-1}$ upstream of the LSZ. Concentrations were not statistically different between stations 3 and 6, which both had significantly lower ($p < 0.05$) concentrations than station 1.

Median chlorophyll *a* concentrations at station 1 in April and May were similar to those measured between 1970 and 1993 in the same section of the channel. In contrast, concentrations were at most half of those previously measured at station 6 (Figures 2 and 3). Concentrations at station 3 were similar to those measured previously in April, but were lower in May.

TABLE 1. Regression Statistics for Log Chlorophyll *a* Consentration and Tidal Velocity Measured at Station 3 during Neap and Spring Tides.

			Spring		
depth	**df**	**intercept**	**slope**	**r squared**	**significance**
1	17	0.63	6.53E-04	0.37	.01
5	17	0.67	4.5E-04	0.31	.02
10	17	0.67	5.42E-04	0.24	.04
all depths	53	0.66	5.86E-04	0.31	.00
			Neap		
depth	**df**	**intercept**	**slope**	**r squared**	**significance**
1	17	0.62	-6.36E-04	0.22	.05
5	17	0.60	-5.60E-04	0.11	ns
10	17	0.70	-3.27E-04	0.06	ns
all depths	53	0.64	-5.69E-04	0.12	.01

FIGURE 2. Median Chlorophyll *a* Concentration across the LSZ in April and May.

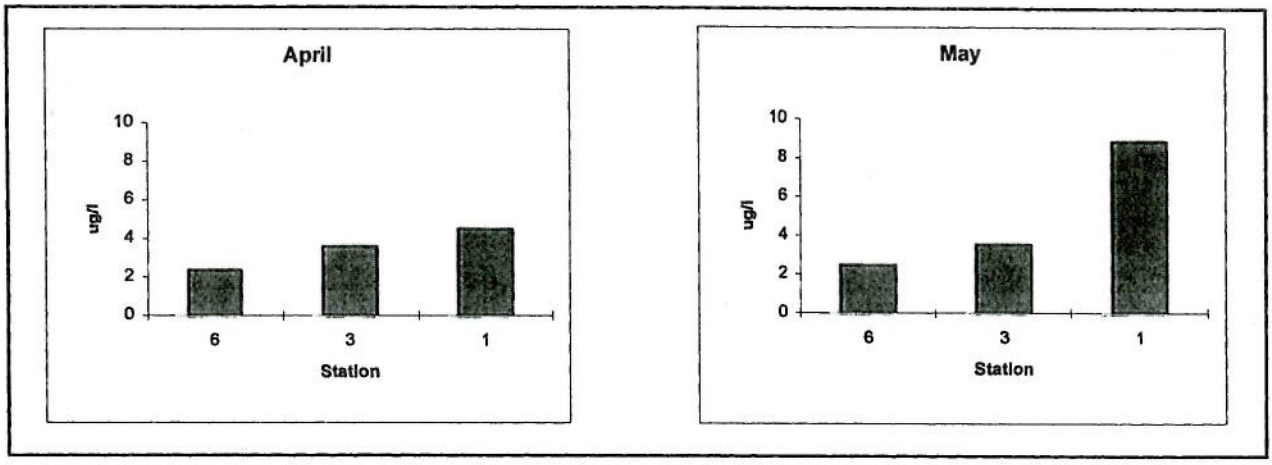


FIGURE 3. Mean and Standard Deviation of Chlorophyll *a* Concentrations Measured at DFG Monitoring Stations between 1970 and 1993 Corresponding to the Section of the Channel between Stations 6 and 1.

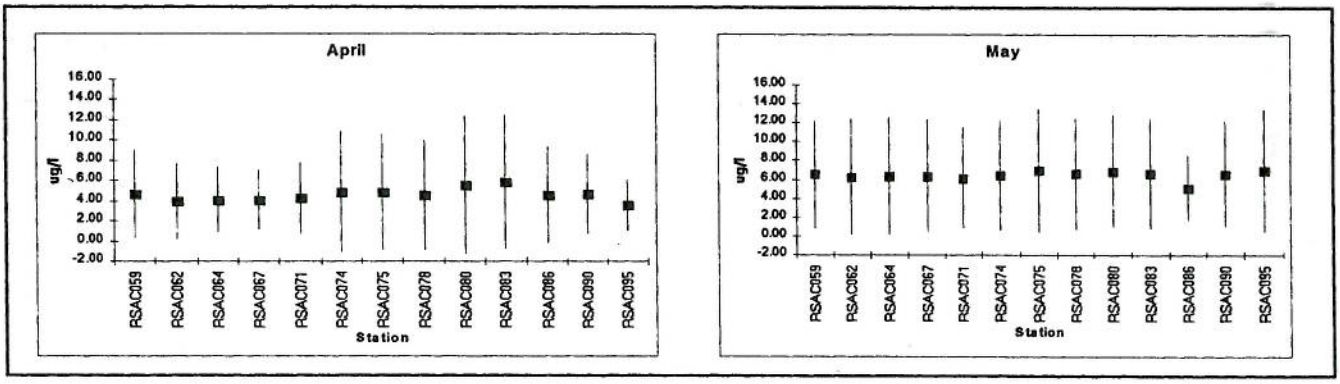
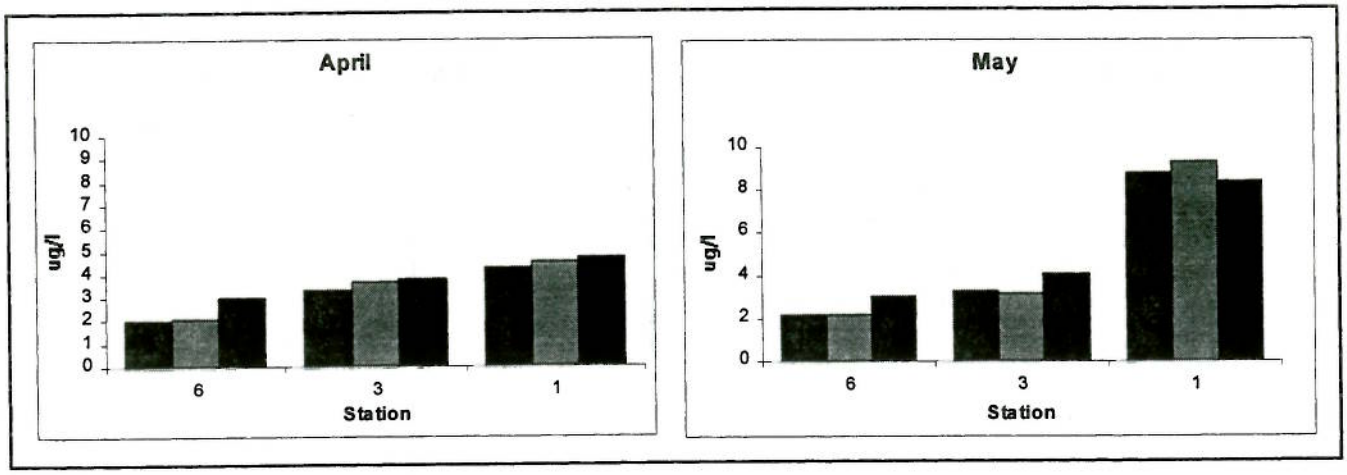


FIGURE 4. Median Chlorophyll *a* Concentrations among Depths across the LSZ.



Chlorophyll *a* concentrations in the LSZ increased with depth and tide. Chlorophyll *a* concentration was up to 32% higher at mid-depth or bottom at stations 3 and 6 (Figure 4). At station 3, concentrations were higher ($p < 0.05$) at both mid-depth and bottom in April and at the bottom in May. At station 6, concentrations were significantly higher ($p < 0.05$) at the bottom in April and the median was 30% higher at the bottom in May. Reduced tidal velocities with depth may have caused higher concentrations near the bottom. Multiple regression coefficients (r^2) for regressions between chlorophyll *a* concentration and tidal velocity were significant only at surface and mid-depth and decreased with depth (Table 1). The increased vertical mixing of the spring tide in April may also have contributed to an increase in chlorophyll *a* concentration near the bottom by resuspension of phytoplankton cells off the bottom on flood tide. Optical backscatter data (OBS) suggest suspended solids were higher in the water column on flood tide in April (Figure 5). Tides further concentrated chlorophyll *a* at the center of the LSZ, where concentrations were up to three times higher ($p < 0.05$) at maximum flood in April during the spring tide and at maximum ebb in May during the neap tide (Figure 6).

FIGURE 5. Vertical Optial Back Scatter Data (OBS) at Ebb (a) and Flood (d) Tide in April. (Figure courtesy of J. Burau.)

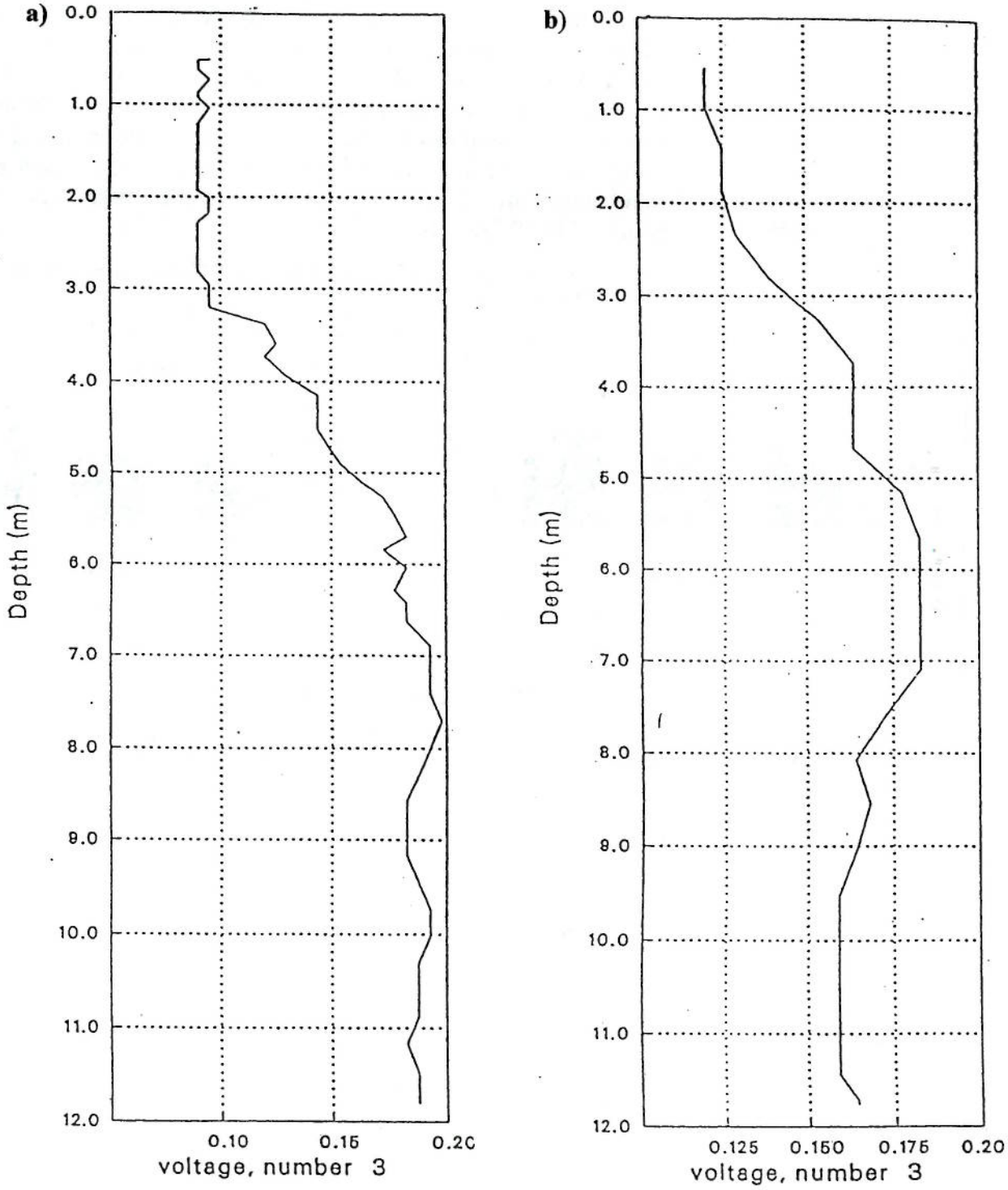
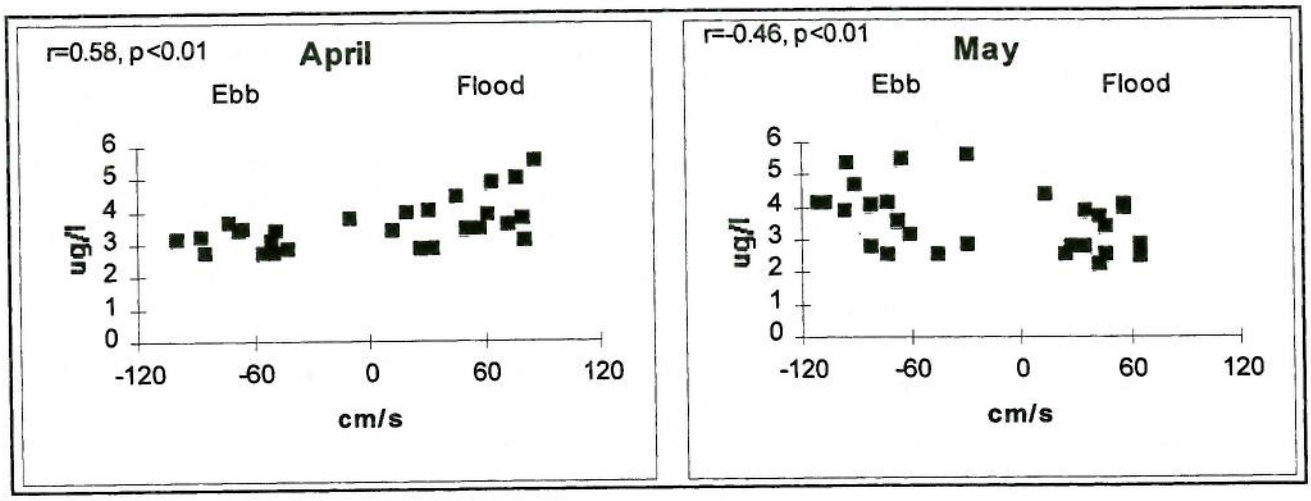


FIGURE 6. Variation of Chlorophyll *a* Concentration with Tidal Velocity at Station 3.



PHYTOPLANKTON SIZE STRUCTURE

The seaward decrease in chlorophyll *a* concentration was accompanied by a decrease in phytoplankton cell diameter. In April, median cell diameter was highest ($p < 0.05$) at station 1, which contained 45% of the microplankton and 85% of the microplankton plus nanoplankton in the LSZ (Figure 7). Median cell diameter was smallest ($p < 0.05$) at station 6, where 40% of the ultraplankton 70% of the ultraplankton plus nanoplankton occurred. In May, median cell diameter was also significantly higher ($p < 0.05$) at station 1, which contained 50% of the microplankton in the LSZ, and decreased seaward ($p < 0.05$). Nanoplankton and ultraplankton were not significantly different among stations.

The high percentage of nanoplankton and ultraplankton in 1994 was part of a long-term increase in the number of small diameter cells in the channel between 1975 and 1993 (Figure 8). Ratios of 5-20 μm to >20 μm sized cells were higher after 1983 ($p < 0.05$) at long-term DWR monitoring stations D8 (near station 6) and D4 (near station 1) during April and May and increased over time at both stations in April (Kendall Tau b, $p < 0.01$). The increase in small diameter cells, however, was probably greater than the long-term monitoring data suggested, because the magnification (750X) used for the monitoring data was too low to quantify <7 μm diameter cells.

Chlorophyll *a* size fraction measurements indicated that phytoplankton size structure varied with both depth and tide at the center of the zone. At station 3, nanoplankton biomass tended to be higher at

mid-depth and bottom in April and was significantly higher ($p < 0.05$) at the bottom in May. In contrast, ultraplankton biomass was evenly distributed in April, but was significantly higher ($p < 0.05$) near the surface in May (Figure 9). Microplankton biomass was not significantly different among depths, but the median tended to be higher at the bottom in May. Tide accumulated microplankton and nanoplankton biomass in a fashion similar to total chlorophyll *a* biomass. Nanoplankton biomass was significantly higher ($p < 0.05$) on flood tide during the spring tidal cycle in April and both microplankton and nanoplankton were significantly higher ($p < 0.05$) on ebb tide during the neap tidal cycle in May (Figure 10).

FIGURE 7. Percent Density of Micro-, Nano-, and Ultraphytoplankton in the LSZ at Each Station in April and May 1994.

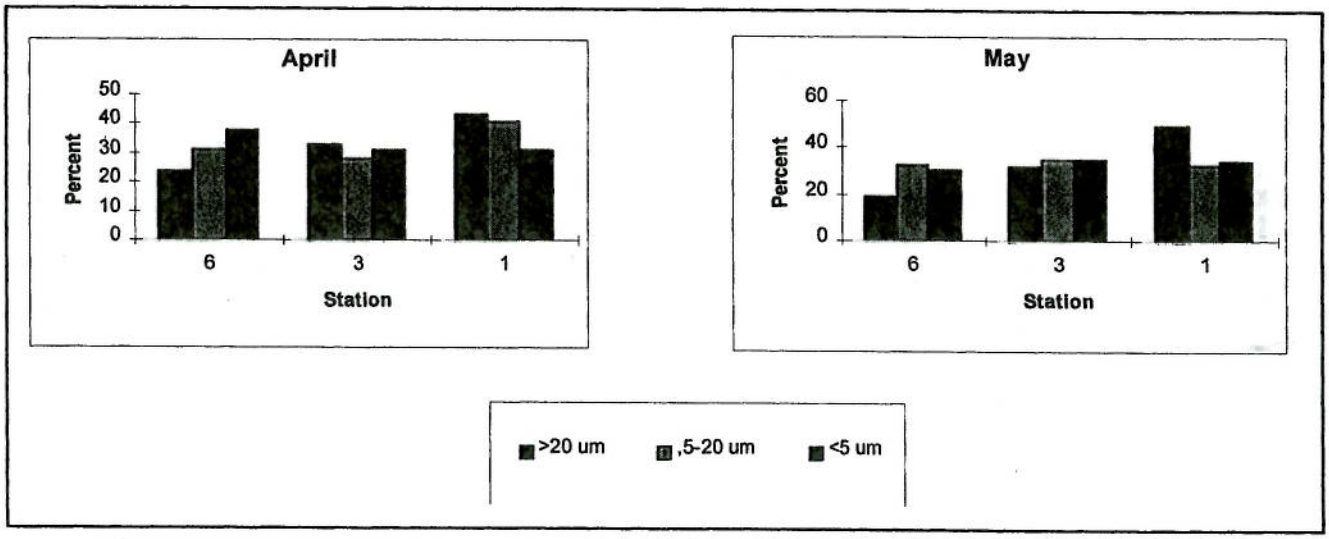


FIGURE 8. Ratio of Nano- (5-20 μm) to Micro- (>20 μm) Phytoplankton Over Time in April and May at Channel Stations D4 and D8.

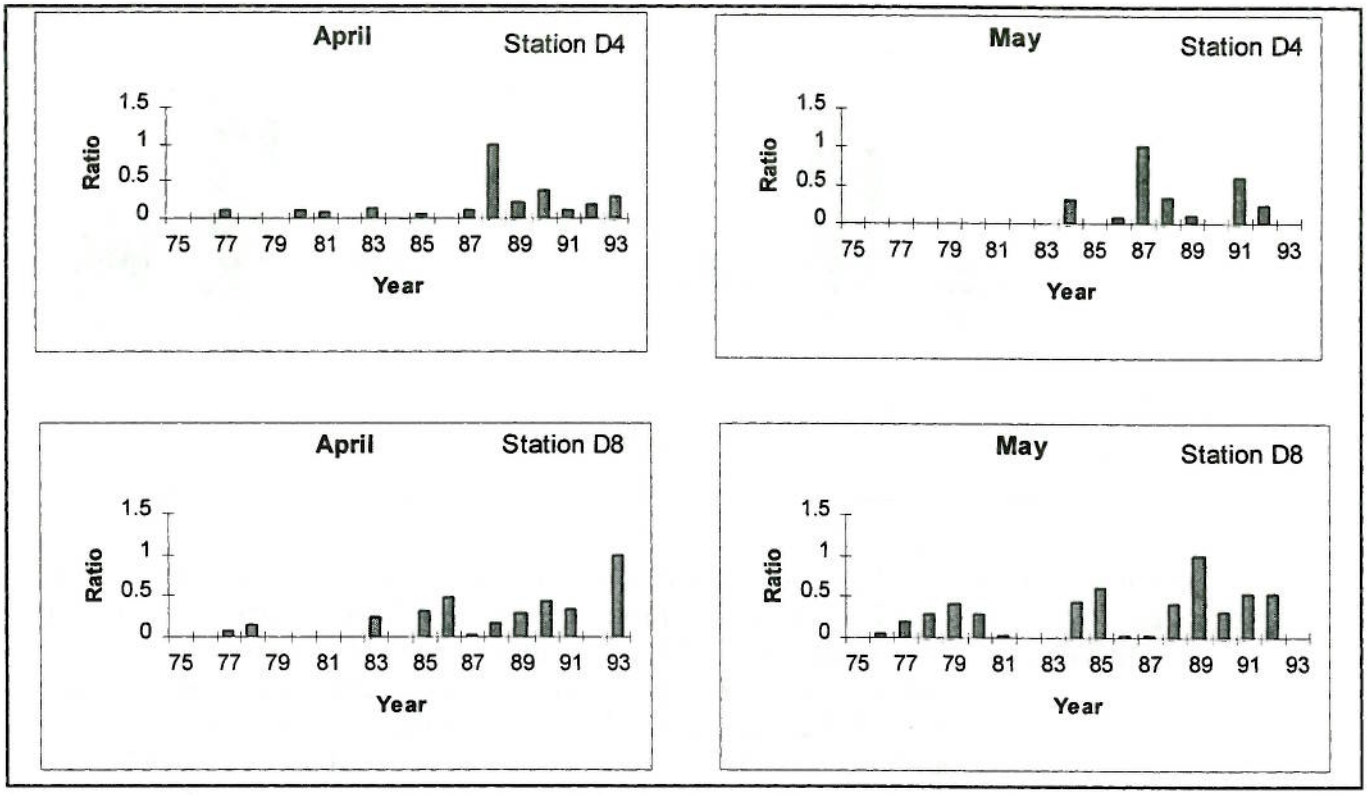


FIGURE 9. Chlorophyll *a* Concentrations in Micro-, Nano-, and Ultraplankton Size Fractions among Depths at Station 3 in April and May 1994.

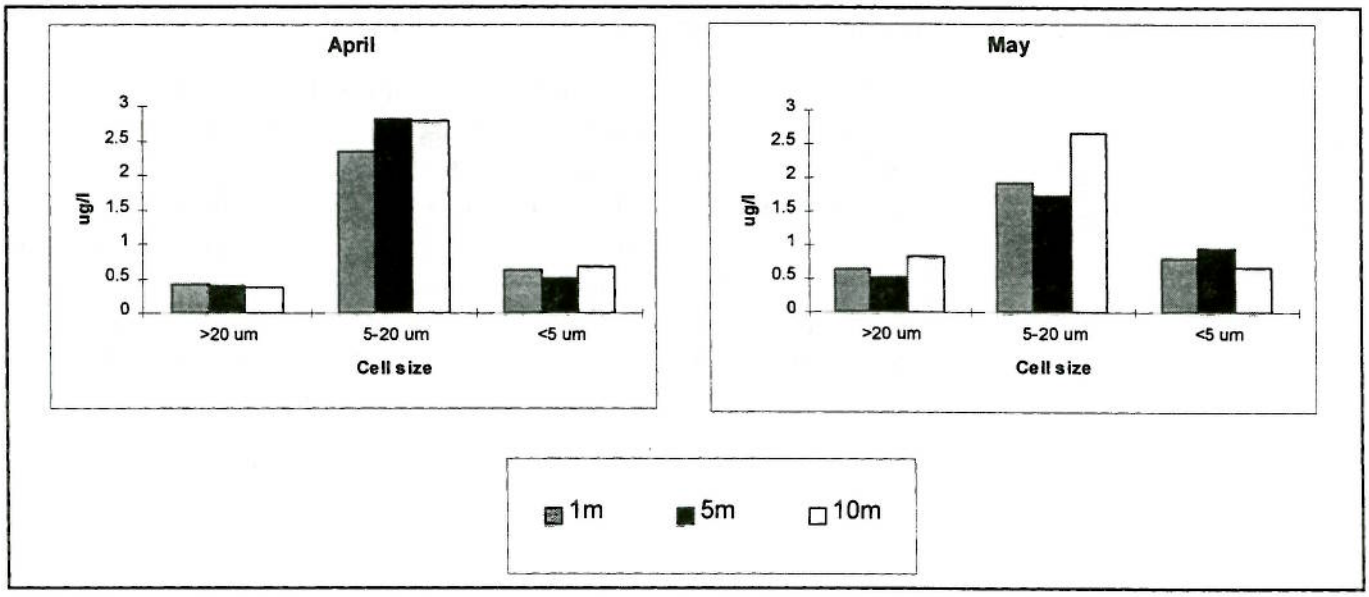
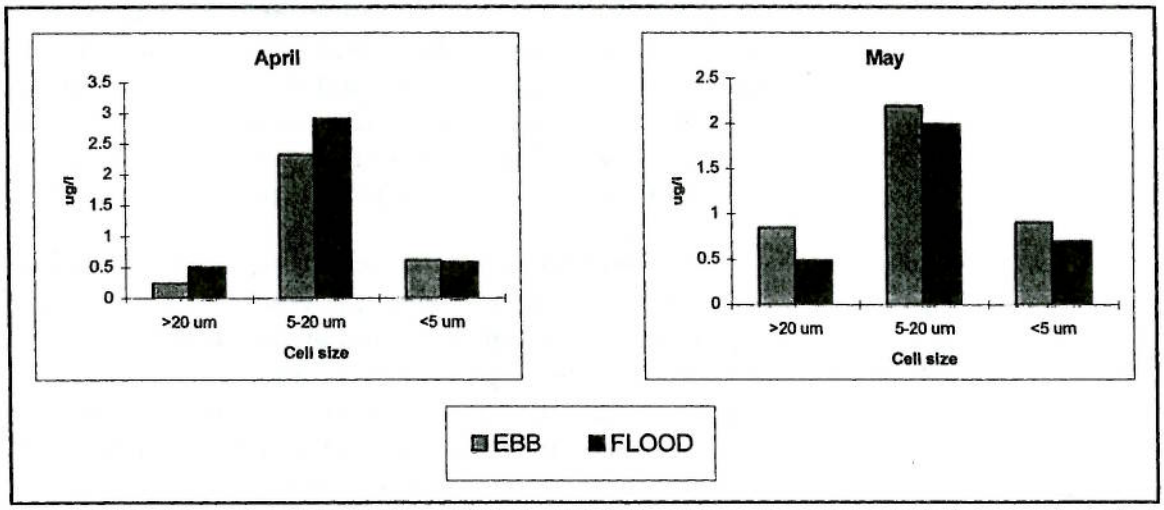


FIGURE 10. Chlorophyll *a* Concentrations in Micro-, Nano-, and Ultraplankton Size Fractions at Ebb and Flood Tide in April and May 1994.

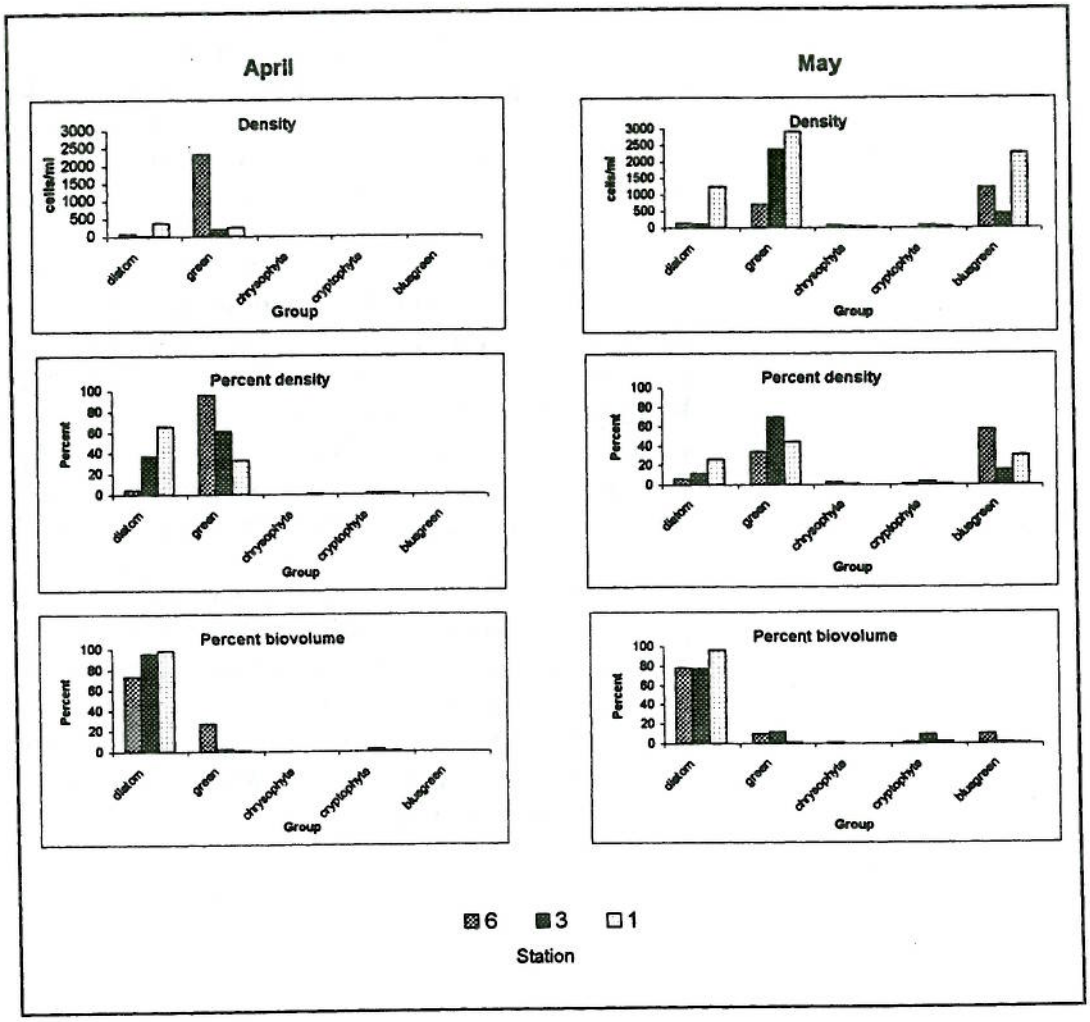


PHYTOPLANKTON SPECIES DENSITY AND BIOVOLUME

Phytoplankton community composition varied across the LSZ. In April, diatoms were most abundant ($p < 0.05$) at station 1, where they comprised nearly 97% of the biovolume and decreased seaward across the zone (Figure 11). In contrast, green algae were most abundant ($p < 0.05$) at station 6, where they comprised 30% of the biovolume, and decreased landward across the zone. In May, green and bluegreen algae were the most abundant phytoplankton throughout the zone. At least half of the cells were green algae at stations 1 and 3, and bluegreen algae at station 6. Diatoms continued to be most abundant at station 1 and comprised at least 70% of the biovolume at all stations.

Ten species comprised at least 10% of the density or biovolume of the phytoplankton in the LSZ. Among these, the ultraplankton, *Nannochloris* spp. (<3 μm diameter), a green alga, and *Synechococcus* spp. (<2 μm diameter), a bluegreen alga, were the most abundant (Figure 12), reaching densities of 2000-4000 cells ml^{-1}. The other abundant genera were microplankton and nanoplankton centric diatoms in the genera—*Aulacoseira*, *Coscinodiscus*, *Cyclotella* and *Thalassiosira*. These genera were far less abundant than green and bluegreen algae; the maximum density reached by *A. granulata* was only 900 cells ml^{-1}.

FIGURE 11. Density, Percent Density, and Biovolume of Phytoplankton Species Groups at Stations 6, 3 and 1 in the LSZ during April and May 1994.



The density and biovolume of these species varied across the LSZ. In April, *Nannochloris* spp. biovolume and density was highest ($p < 0.01$) at station 6 where it comprised 94% of the cells and up to 27% of the biovolume, compared with 30-45% of the density and < 5% of the biovolume at station 1 and 3 (Figure 12). Diatoms, like *Cyclotella striata* and *Coscinodiscus excentricus* were most abundant ($p < 0.01$) at station 1 where they comprised 10-40% of the density and 15-45% of the biovolume. *Thalassiosira decipiens* was also most abundant at station 1, and decreased ($p < 0.01$) seaward across the zone. Only the large diatom (> 40 μm diameter), *C. lineatus*, was most abundant ($p < 0.01$) at station 6, where it comprised 10% of the biovolume. At the center of the zone, each diatom species comprised 10-15% of the density or bio-

volume. In May, *Nannochloris* spp. comprised 40-60% of the cells at all stations and was accompanied by *Synechococcus* spp., which comprised up to 30% of the cells at station 6. *Aulacoseira granulata* was abundant and comprised most of the biovolume in the zone. Density and biovolume were highest at station 1 and decreased ($p < 0.01$) across the zone. In contrast, *C. excentricus*, *C. lineatus* and *C. meneghiniana* density and biovolume were highest at station 6 where they each comprised only $< 10\%$ of the density and up to 20% of the biovolume.

Phytoplankton species composition also varied somewhat with depth and tide. *Nannochloris* spp. tended to be more abundant at mid-depth and bottom in April and at the surface and mid-depth in May (Figure 13). The large diatom *C. lineatus* was higher ($p < 0.01$) at the bottom while the small diatom *C. meneghiniana* and *T. decipiens* tended to be near the surface and mid depth in April. The most abundant diatom *A. granulata* was most abundant ($p < 0.05$) at the surface at stations 3 and 6 and at the bottom at station 1 in May.

Between tides, *Nannochloris* spp. followed the pattern of chlorophyll *a* concentration and was often more abundant on flood tide in April during the spring tide and on ebb tide in May during the neap tide (Figure 14). The diatoms, *C. striata* and *C.* at station 1 and *T. rotula* ($p < 0.05$) and *C. meneghiniana* at station 3 in April were more abundant on ebb tide. At station 1 in May, *A. granulata* was more abundant ($p < 0.05$) on flood tide.

FIGURE 12. Percent Density and Biovolume of Phytoplankton Species Comprising more than 10% of the Density or Biovolume at Stations 6, 3, and 1 in the LSZ during April and May 1994.

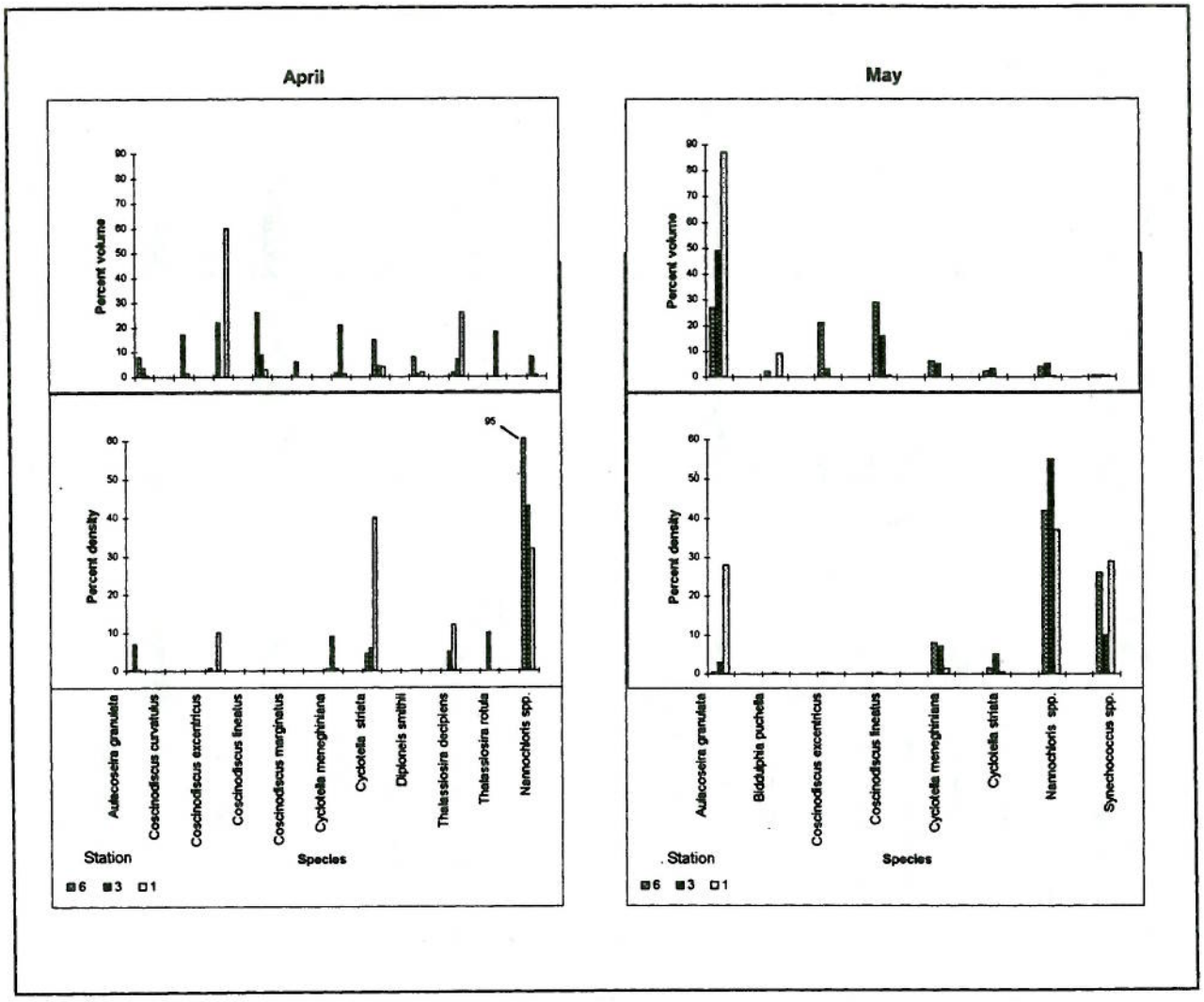


FIGURE 13. Percent Density and Biovolume of Phytoplankton Species Comprising more than 10% of the Density or Biovolume among Depths at Stations 6, 3, and 1 in the LSZ during April and May 1994.

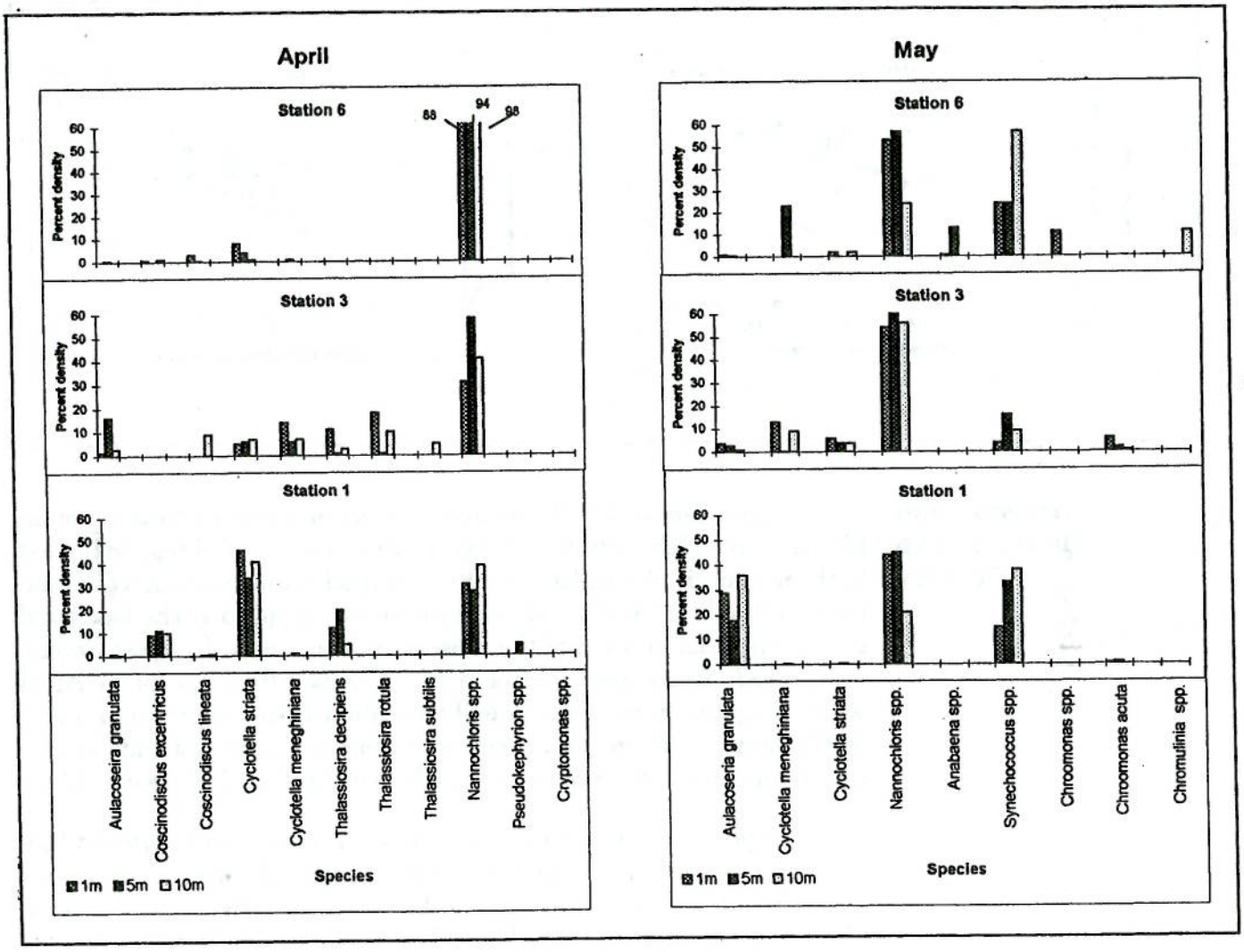


FIGURE 14. Percent Density of Phytoplankton Species Comprising more than 10% of the Density on Ebb and Flood Tides at Stations 6, 3, and 1 in the LSZ during April and May 1994.

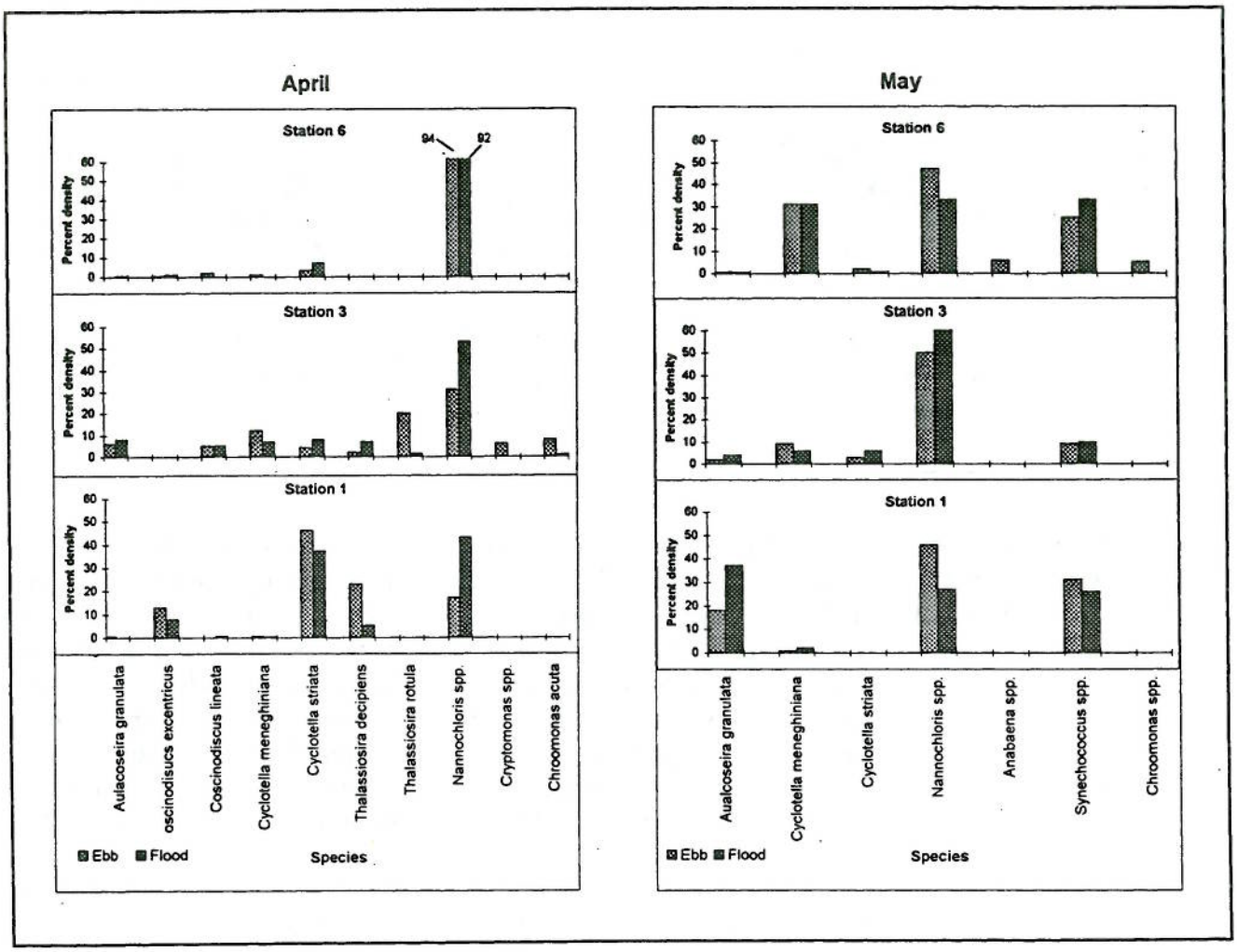
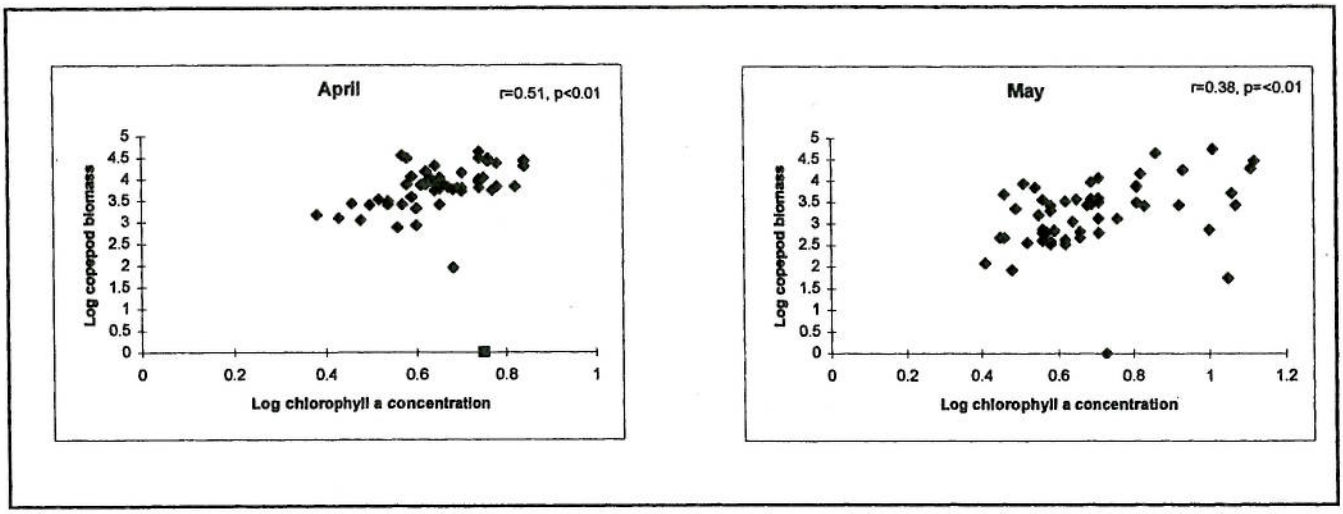


FIGURE 15. Variation of Copepod Biomass ($\mu g\ C1^{-1}$) and Chlorophyll *a* Concentration ($\mu g\ 1^{-1}$) in April and May 1994.



COPEPOD FOOD QUANTITY AND QUALITY

A significant ($p < 0.01$) positive correlation between total copepod biomass and chlorophyll *a* concentration among stations, indicated both maximum phytoplankton and copepod biomass occurred at station 1 (Figure 15). Over 55% of the biomass occurred at the landward edge of the LSZ for each of the most abundant copepods, *Pseudodiaptomus forbesi*, *Sinocalanus doeri* and *Eurytemora affinis*; except in April when *E. affinis* biomass was equally distributed between stations 1 and 3. Maximum total biomass occurred at station 1 despite a shift in species dominance in the LSZ from *E. affinis* in April to *P. forbesi* in May.

The poor match between the vertical distribution of copepod biomass and chlorophyll *a* concentration or chlorophyll *a* size fractions was probably a function of the variability produced by copepod vertical migration. Higher ($p < 0.05$) total copepod biomass at night, and the tendency for median copepod biomass to be higher at mid-depth and bottom during the day and at the surface during the night, suggests copepods migrated vertically (Figure 16). Migration to the surface would probably not increase the quantity of food available at night for copepods at the center or seaward edge of the zone, where highest chlorophyll *a* concentrations were near mid-depth and bottom (Figure 4). Neither would it increase the availability of microplankton or nanoplankton chlorophyll *a* size fractions that were higher near the bottom (Figure 9). Vertical migration would expose copepods to higher tidal velocities near the surface that would move them horizontally with the

tide, but not necessarily toward higher chlorophyll *a* concentration (Figure 6).

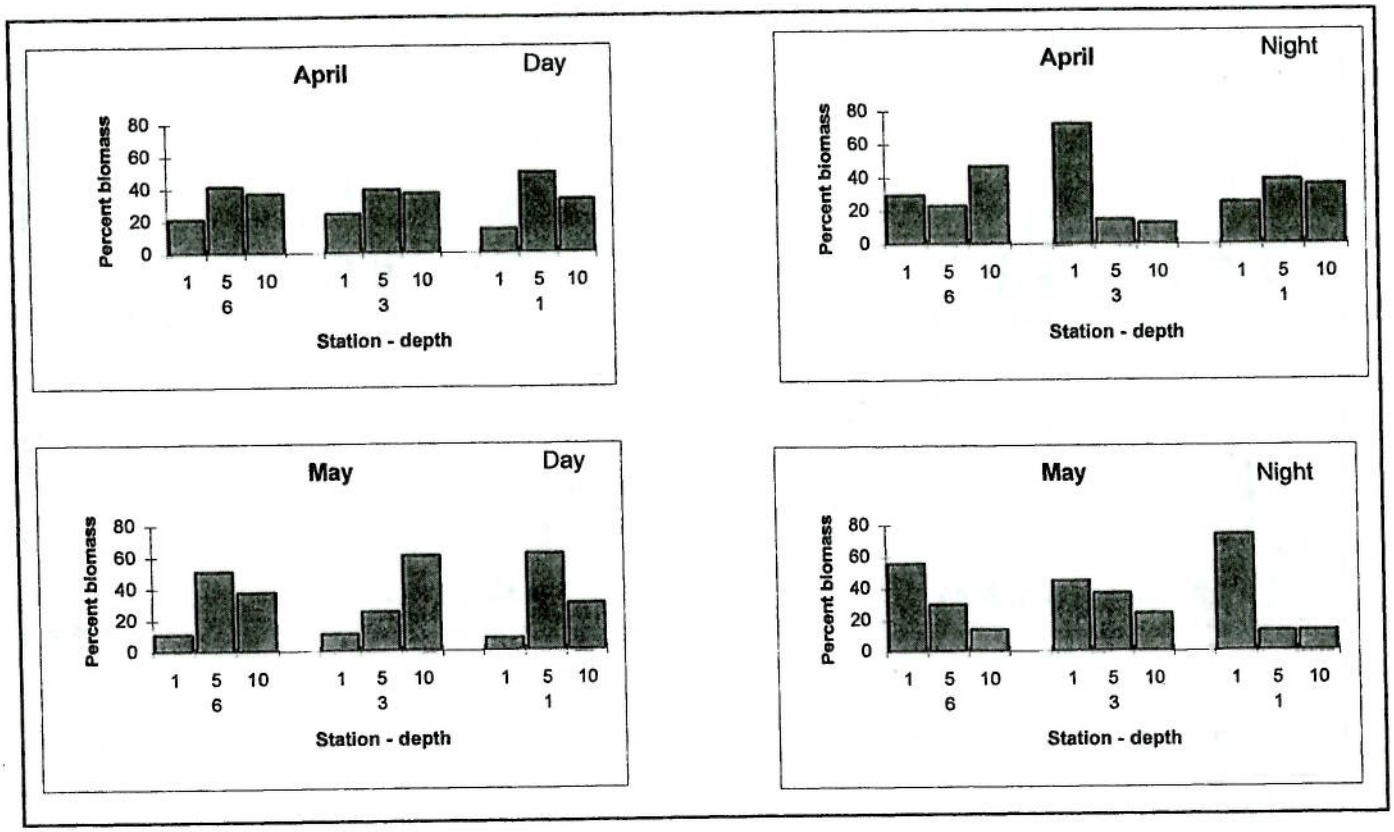
Size structure of the phytoplankton community may have affected food quality for copepods, which are size selective feeders. In general, optimum predator/prey ratios based on ESD values are 10-33:1 for adults and 9-23:1 for copepodids (Hansen et al. 1994). For copepods in this study, optimum predator/prey ratios require phytoplankton ESD values in the range of 10.5-43.0 μm for adults and 10-29 μm for copepodids (Table 2). *P. forbesi* females that have optimum phytoplankton prey ESD values between 14.5 and 43.4 μm require the largest phytoplankton cells.

Many phytoplankton cells fell within the preferred ESD size range for adults and copepodids at station 1, where at least 45% of the cells were >10 μm (ESD) (Figure 17) and contrasted with station 6, where only a few percent of the cells had ESD values >10 μm. Station 3 had cells with the optimum ESD size in April, but few in May. These ESD values were reflected in the median predator/prey ratios that were within the optimum size range for adult and juvenile copepods at stations 1 and 3 in April, but not in May; only about 10-25% of the ratios fell within the optimum range at station 1 in May (Figure 18). Historical data indicated ESD values were often low (<10 μm) in the channel and decreased over time in April (Kendall Tau b, $p < 0.05$) at monitoring stations D8 and D4 (near stations 6 and 1, respectively).

TABLE 2. Copepod Dry Weight, Carbon, Volume and ESD, and Phytoplankton ESD Needed for Optimal and Predator/Prey Ratios.

Species	Mean dry weight (μg)	Range dry weight (μg)	Mean carbon (μg)	Range carbon (μg)	Mean volume (μm^3)	Range volume (μm^3)	Mean ESD (μm^3)	Range ESD (μm^3)	Phyto ESD range (μm)
Eurytemora affinis —female	7.00	5.5-8.5	3.15	2.48-3.82	2.63E+07	2.06E+3.19 E+07	347.70	321.10-370.71	11.59-34.77
Eurytemora affinis —male	5.25	4.5-6.0	2.36	2.02-2.70	1.97E+07	1.69E+07-2.25E+07	316.21	300.53-330.46	10.54-31.62
Sinocalanus doerii —female	8.75	7.0-10.5	3.94	3.15-4.72	3.28E+07	2.62E+07-0.39E+07	374.27	347.70-397.48	12.42-37.43
Sinocalanus doerii —male	6.00	5.0-7.0	2.70	2.25-3.15	2.25E+07	1.88E+07-2.62E+07	330.446	31.16-347.70	11.02-33.05
Pseudodiaptomus forbesi-female	13.75	13-14.5	6.19	5.85-6.52	5.16E+07	4.88E+07-5.44E+07	434.47	426.51-442.16	14.48-43.45
Pseudodiaptomus forbesi-male	7.40	6.8-8.0	3.33	3.06-3.6	2.78E+07	2.55E+07-3.00E+07	354.14	344.39-363.37	11.80-35.41
Copepodids	3.00	-	1.35	-	1.12E+07	-	262.00	-	10.0-29.0

FIGURE 16. Median Percent Total Copepod Biomass among Depths at Stations 6, 3, and 1 across the LSZ during April and May 1994.



Availability of >10 μm diameter phytoplankton cells was affected by their production rate which was highest and more closely matched to copepod production rate at station 1. Production rates of >10 μm diameter phytoplankton cells decreased seaward across the LSZ; 11, 2 and 1 mg C m^{-2} day^{-1} in April and 64, 3 and 0.3 mg C m^{-2} day^{-1} in May. Production rates for copepods also decreased seaward across the LSZ; 14, 7 and 2 mg C day^{-1} in April and 7, 1 and 0.4 mg C day^{-1} in May. In April when copepodids were abundant, phytoplankton carbon was lower than copepod carbon at all stations, but the difference between phytoplankton and copepod carbon was smallest at station 1. In May, phytoplankton carbon exceeded copepod carbon only at station 1 and 3. For both months, the production rate of >10 μm diameter cells at station 6 was consistently lower than that needed by copepods.

Median predator/prey ratios varied somewhat with depth and tide. Among depths median, predator/ prey ratios were within the optimum range in April at all depths at station 1, the surface and bot-

tom at station 3 and no depths at station 6 (Figure 19). In May, individual or median predator/prey ratios were within the optimum range at all depths at station 1 and at the surface at station 3. No ratios were within the optimum range at station 6 for either adults or copepodids. Among tides, median predator/prey ratios were within the optimum range on ebb tide in April at stations 1 and 3, but were above the optimum range on flood tide. No ratios were within the optimum range at station 6 on flood or ebb tide. In May, median predator/prey ratios were above optimum values at all stations, but some ratios within the optimum range at station 1 (Figure 20).

In addition to their influence on size structure, small-scale spatial and temporal variations in phytoplankton species composition can affect copepod food quality, because each phytoplankton species has different physical and chemical characteristics. Potentially important characteristics for the SFBE are listed in Table 3, and suggest that food quality might not have been optimal at all times, even at the landward edge of the LSZ where diatom density and chlorophyll *a* concentration were high.

FIGURE 17. Percent Phytoplankton in ESD Size Categories at Stations 6, 3, and 1 across the LSZ in April and May 1994.

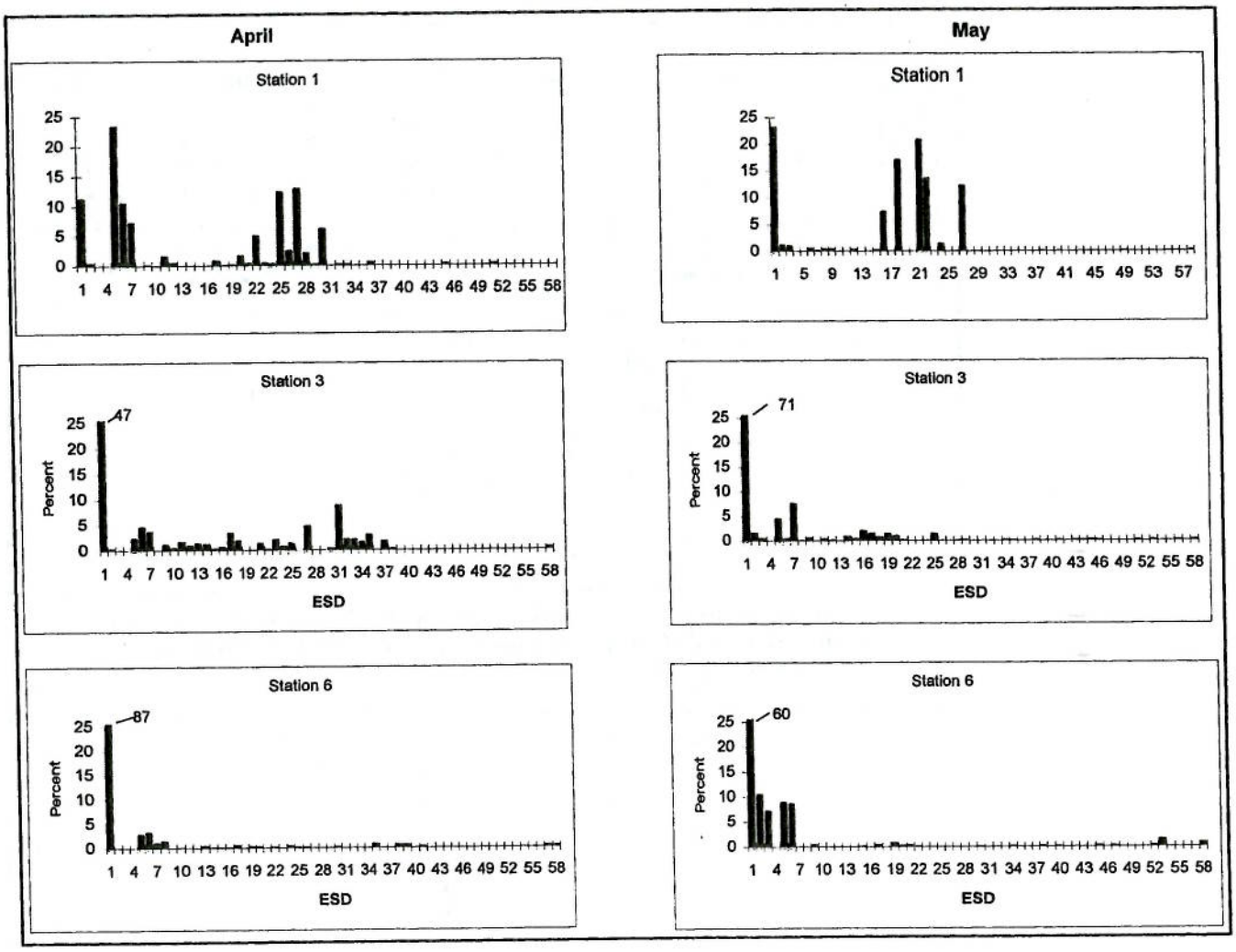


FIGURE 18. Median, 5th and 95th Percentiles for Predator/Prey Ratios of Adult and Juvenile Copepods at Stations 6, 3 and 1 Across the LSZ in April and May 1994.

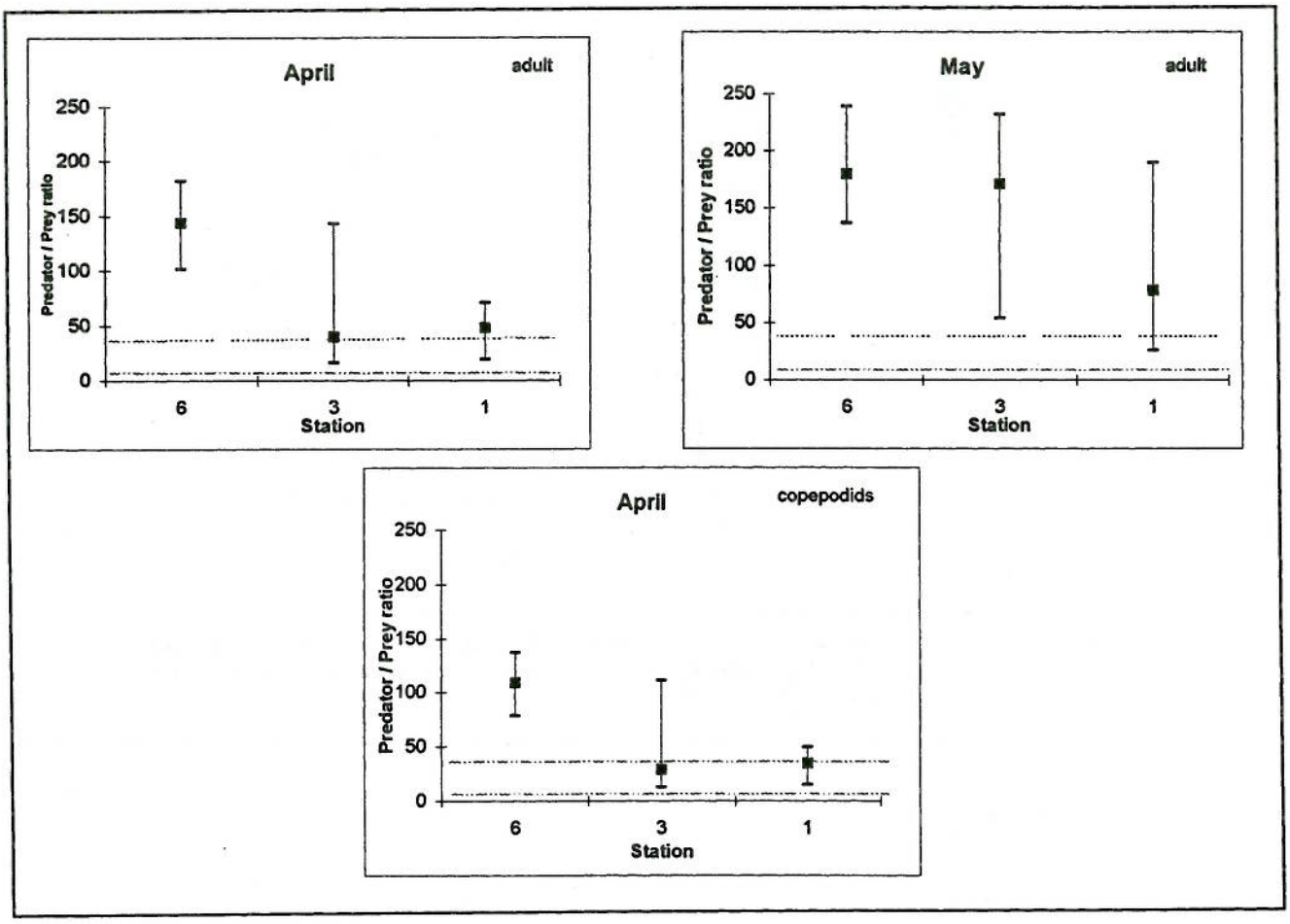


FIGURE 19. Median, 5th, and 95th Percentiles for Predator/Prey Ratios of Adult and Juvenile Copepods Among Depths at Stations 6, 3, and 1 across the LSZ in April and May 1994.

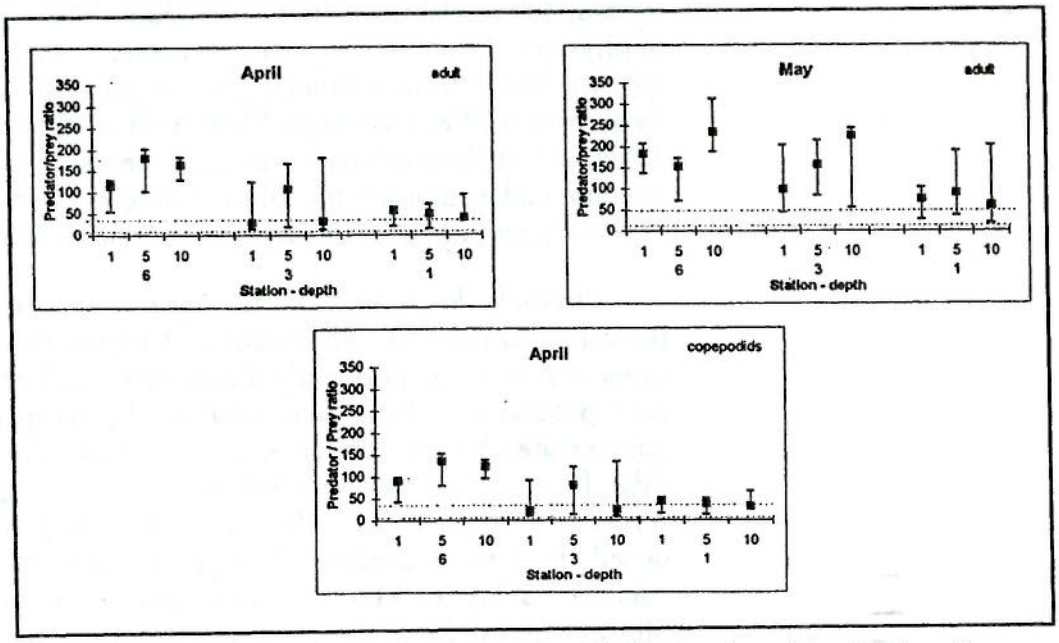


FIGURE 20. Median, 5th, and 95th Percentiles for Predator/Prey Ratios of Adult and Juvenile Copepods across the LSZ on Ebb and Flood Tide in April and May 1994.

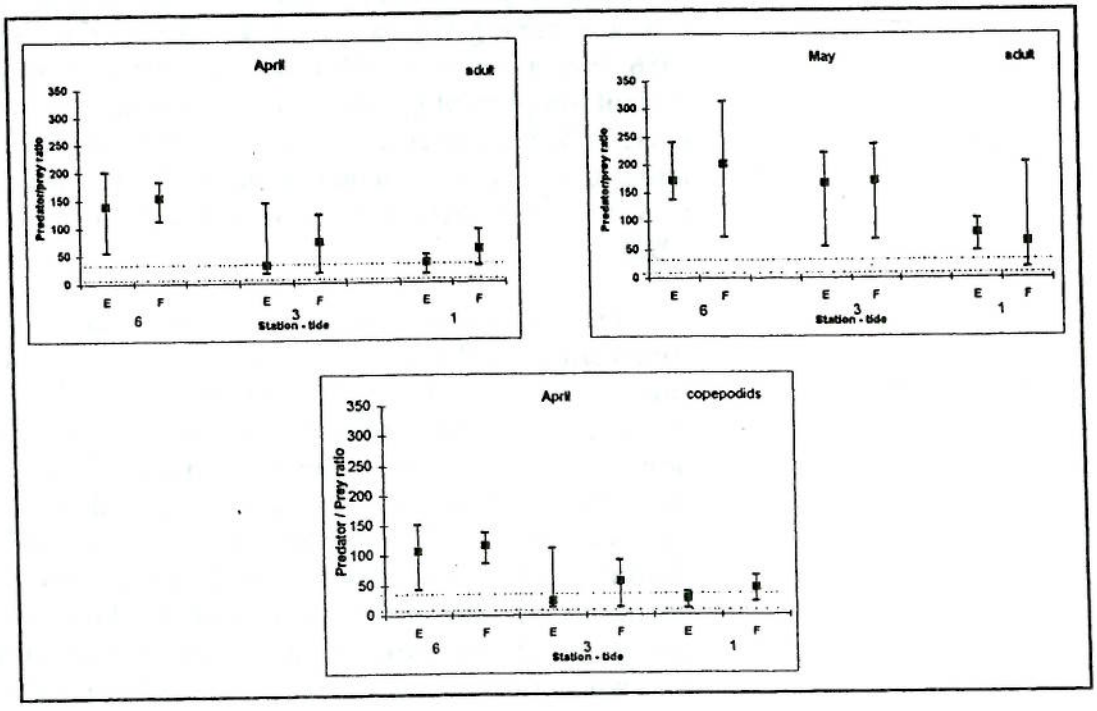


TABLE 3. Unfavorable Physical and Chemical Characteristics of Phytoplankton Species as Food for Copepods.
Phytoplankton are listed which comprised 5% or more of the total biomass of density across the salinity gradient.

Characteristics	Species	References
Contains toxins which inhibit egg production and viability	*Thalassiosira rotula*	Poulet et al. 1994
Forms chains which mechanically intefere with feeding	*Aulacoseira granulata, Thalassiosira decipiens, T. routla, Cosinodiscus lineatus*	Paffenhoffer 1971; Gliwicz 1980; McNaught et al. 1980; Hartman 1985; Fulton 1988
Poorly digested or utilized	*Synechococcus* spp., *Anabaena* spp.	Porter 1973; Ianora and Poulet 1993; Twombly and Burns 1996
Cell diameter too small or too large	*Synechococcus* spp., *Nannochloris* spp., *Coscinodiscus lineatus*	Paffenhoffer and Knowles 1978; Kiorboe et al. 1990; Peterson et al. 1991; Hansen et al. 1994
Small lipid to volume and protein to volume ratio	All diatoms	Kleppel et al. 1991; Ianora and Poulet 1993

Discussion

FACTORS INFLUENCING PHYTOPLANKTON ACROSS THE LSZ

Many physical, chemical and biological factors probably affected phytoplankton biomass, species composition and cell diameter across the LSZ. At the landward edge of the LSZ, the high chlorophyll *a* concentrations, large diameter cells and abundant diatoms were probably advected from upstream phytoplankton communities. Advective transport, particularly on ebb tide, is an important mechanism for transporting chlorophyll *a* downstream in estuaries (Malone 1977; La Fleur 1979; Demers et al. 1986; Dustan and Pickney 1989). In fact, in South San Francisco Bay, chlorophyll *a* concentrations were higher when riverine phytoplankton were transported into the bay on ebb tide (Cloern et al. 1989). That higher chlorophyll *a* concentrations on ebb tide were produced by upstream phytoplankton is supported by the increase of diatoms on ebb tide and green and bluegreen algae on flood tide. In a similar fashion, freshwater species were more abundant downstream on ebb tide in the St. Lawrence (Sinclair 1978; La Fleur 1979; Frenette et al. 1995) and Chesapeake Bay (Seliger et al. 1981) estuaries and coastal phytoplankton were more abundant on ebb tide at tidal fronts (Le Fevre 1986).

The center of the zone was characterized by lower chlorophyll *a* concentrations and diatom densities and smaller diameter cells than at the landward edge of the zone. This was probably due to reduced advective transport from upstream plus the loss of freshwater diatoms that lyse (Small et al. 1990). In addition, freshwater diatoms in Suisun

Bay form aggregates that settle to the bottom in brackish water (Ball and Arthur 1981). *P. amurensis* grazing may further contribute to the loss of diatom cells, but its influence is probably less here than downstream, where clam densities are highest. There was no accumulation of phytoplankton biomass or large diameter diatoms, like *Coscinodiscus* spp. or *Skeletonema costatum,* by gravitational circulation as initially hypothesized (Peterson et al. 1975; Arthur and Ball 1979; Cloern et al. 1983). In fact, hydrodynamic measurements taken during this and subsequent studies indicate the salinity zone in the channel is too small to produce gravitational circulation in the spring (Burau 1998).

Phytoplankton biomass, however, was accumulated with tide at the center of the LSZ. The factor of 3 higher chlorophyll *a* concentrations at maximum flood tide during the April spring tide could have been produced by local accumulation of phytoplankton at the frontal zone created by the convergence of seaward river flow and landward tidal flow, which was magnified by the spring tide (Dustan and Pickney 1989; LeFevre 1986). An opposite process could have produced the 2 times higher chlorophyll *a* concentrations at maximum ebb tide during the May neap tidal cycle, when advective transport of phytoplankton from upstream was enhanced by the seaward flow of both the river and tide, magnified this time by the neap tide (Dustan and Pickney 1989). Changes in phytoplankton biomass with ebb-flood or spring-neap asymmetry have been often been attributed to advection and mixing (Sinclair 1978; La Fleur 1979; Seliger 1981; LeFevre 1986, Frenette et al. 1995). Other potential causes are changes in phytoplankton physiology due to changes in species composition (Demers et al. 1979; Sinclair et al. 1980) or the influence of mixing on light and nutrient availability (Demers et al. 1986). The latter cause is less likely in SFBE where light is limiting and nutrients are in excess (Lehman 1992).

Tidal advection probably also influenced size structure and species composition at the center of the LSZ, where nanoplankton accumulated on flood tide during the spring tidal cycle in April, and microplankton and nanoplankton accumulated on ebb tide during the neap tidal cycle in May. Strong vertical mixing associated with the spring tide may also have increased nanoplankton cells near the bottom by resuspension. The most abundant cells at the bottom were nanoplankton and their density increased during the spring flood when sediments were higher in the water column. The strong vertical mixing of the spring tide was probably necessary to resuspend cells near the bottom where tidal velocities are low. Research has demonstrated changes

in phytoplankton species composition and size structure from tidal advection (Sinclair 1978; LaFleur 1979; Sinclair et al. 1980; Frenette et al. 1995) and mixing (Levasseur et al. 1984; Demers et al. 1986; Turpin and Harrison 1980).

At the seaward edge of the LSZ, grazing by *P. amurensis* may be an overriding influence on phytoplankton biomass, species composition and size structure. The ability of *P. amurensis* to remove phytoplankton biomass from the water column is very high. Since its introduction in 1987, it has lowered chlorophyll *a* concentrations in Suisun Bay by a factor of 10 from >20 to <3 $\mu g\ l^{-1}$ (Nichols et al. 1990; Alpine and Cloern 1992). Its ability to remove phytoplankton in channels is a function of high densities which reach 6000 clams m^{-2} in drought years (DWR, unpublished data), and high grazing rates, that enable it to filter water in 10 m deep channels 1.28 times per day (Werner and Hollibaugh 1993). In April and May 1994, clam densities reached up to 912 clams m^{-2} in Suisun Bay and decreased landward (stations D4 and D7, DWR, unpublished data). The clams may have an equally large effect on phytoplankton cell diameter and species composition. Species identifications at high magnification (1000X) indicate the LSZ had large diameter (>20 μm) marine diatoms in the 1970s (Arthur and Ball 1979; Cloern 1979; Cloern et al. 1983; Wong and Cloern 1981). But during this study, species identifications at similar magnification indicated at least 70% of the phytoplankton were the green and bluegreen ultraplankton (1-3 μm diameter), *Nannochloris* spp. and *Synechococcus* spp. The ultraplankton may persist because they are inefficiently grazed by *P. amurensis*, which have poor retention of <5 μm diameter cells (Werner and Hollibaugh 1993).

The low median chlorophyll *a* concentrations at the center and seaward edge of the LSZ were augmented by up to a 30% higher phytoplankton biomass with depth. Higher chlorophyll *a* concentration at the bottom was also measured in this region during the 1970s (Arthur and Ball 1979; Ball and Arthur 1979) and is similar to the increase in biovolume at the bottom with distance downstream in the St. Lawrence (Frenette et al. 1995). Settling rates of 2-6 m day^{-1} promote rapid settling of large and medium sized cells in San Francisco Bay (Ball and Arthur 1981) and may explain why the largest diatom in the LSZ, *Coscinodiscus lineatus*, was more abundant at the bottom. However, most of the cells at the bottom were nanoplankton. Settling of these cells is enhanced in by cell aggregations produced when freshwater phytoplankton encounter brackish water (Ball and Arthur 1981).

An increase in large diameter cells at the bottom in the St. Lawrence estuary was also attributed to sedimentation and resuspension (Frenette et al. 1995) and a horizontal salinity shear that traps cells at the bottom (Therriault et al. 1990). These factors may also be important in the LSZ, where the water column was characterized by a relatively small vertical salinity gradient as well as reduced velocities near the bottom (Burau 1998). The increase in chlorophyll *a* concentration near the bottom seems to contradict the influence of clam grazing on phytoplankton chlorophyll *a* concentrations. However, it is likely that chlorophyll *a* concentrations decrease closer to the clam bed than was sampled and that lower filtration rates of clams early in the year, when water temperatures are low (Werner and Hollibaugh 1993) and clams are small (J. Thompson, personal communication) reduce their influence.

COPEPOD FOOD QUANTITY AND QUALITY

Phytoplankton biomass was probably not limiting to copepods at the landward edge of the LSZ, but may have been sufficiently low at the center and seaward edge of the LSZ to limit or reduce copepod egg production and viability or growth rates in the spring. Chlorophyll *a* concentrations at or below 0.5-2.5 $\mu g\ l^{-1}$ were associated with decreased growth rate or poor egg production in the copepods, *Acartia tonsa*, *A. clausi*, *Temora longicornis*, *Pseudocalanus* sp., *P. parvus*, and *Calanus finmarachicus* (Klein Breteler et al. 1982; Durbin et al. 1983; Kiorboe and Johansen 1986; Berggeen et al. 1988; Kiorboe et al. 1990; Peterson et al. 1991). In addition, egg production rates for these species increased with increasing chlorophyll *a* concentrations. Because the median and range of chlorophyll *a* concentrations at the landward edge of the LSZ were above these threshold values, they probably did not limit copepod growth or egg production (Klein Breteler et al. 1982; Durbin et al. 1983; Berggeen et al. 1988). This may partially explain why maximum total copepod biomass consistently occurred at the landward edge of the LSZ.

In contrast, the median and range of chlorophyll *a* concentrations at the seaward edge of the LSZ fell below or near these threshold values and may affect copepod growth and egg production. Adverse affects of low chlorophyll *a* concentrations at the center and seaward edge of the LSZ, however, were probably reduced by accumulation of phytoplankton with depth and tide. Small-scale and periodic increases in phytoplankton biomass (Wangersky 1974) and increases in biomass with depth (Strickland 1968) can increase food availability for copepods by many times. This additional accumulation of chlorophyll *a* concentra-

tion is important for copepods at tidal fronts where it coincides with peak egg production (Kiorboe and Johansen 1986; Kiorboe et al. 1988).

Chlorophyll *a* concentration, however, was not always the best indicator of phytoplankton food availability in the LSZ. Small ESD values and large predator/prey ratios indicated copepods had unfavorable food at the center and seaward edge of the LSZ, because of the dominance of small diameter cells. The opposite occurred at the landward edge of the LSZ. Copepods are size selective feeders and adults prefer phytoplankton with cell diameters between 8 and 40 μm (Kiorboe et al. 1990; Peterson et al. 1991) and predator/prey values between 10 and 30:1 (Hansen et al. 1994). The range of these cell sizes agrees with the cell diameters of phytoplankton found in the guts of *E. affinis* and *S. doerii* in this estuary (Orsi 1995) and the predator/prey ratio of 22:1 calculated for an average diatom in the estuary and *E. affinis* (Lehman 1996a).

During this study the percent of ESD values <10 μm was 60-80% at the center of the zone and 95-98% at the seaward edge of the zone in April and May. These low ESD values produced predator/prey ratios that were up to an order of magnitude higher than the optimum range for juveniles and adults and may partially explain why the highest copepod biomass coincided with the the highest median phytoplankton cell diameter at station 1. Phytoplankton cell diameter above or below 11-50 μm may reduce or limit maximum copepod egg production rates by 13-50% (Peterson et al. 1991). Similarly, egg production rates were low for *A. clausi* and *T. longicornis* when phytoplankton ESD values were lower than 7 μm (Kiorboe et al. 1990). High production rate of >10 μm diameter phytoplankton cells was probably able to compensate for these high predator/prey ratios only at the landward edge and center of the LSZ in May.

Phytoplankton species composition may have further affected food quality for copepods in the LSZ, but there is no information on their direct effects from this study. Copepods feed selectively on phytoplankton species (Paffenhoffer and Knowles 1978; Peterson et al. 1991; Kiorboe et al. 1990) and the type of phytoplankton eaten can affect molting frequency, growth and mortality rate, and body size (Twombly and Burns 1996). In the SFBE, the optimum food for copepods may be diatoms because the diatoms *Thalassiosira* spp. and *Skeletonema potamos* were the most abundant phytoplankton in the gut of *E. affinis* and *S. doerii* (Orsi 1995) and the wide ell diameter and high cellular biovolume of diatoms maks them an important source of car-

bon (Lehman 1996a). Besides being too small, the abundant green and bluegreen algae in the LSZ were probably not high quality food. Bluegreen algae, such as *Anabaena flosaquae* and *Synechococcus* spp. are often poorly digested by copepods (Porter 1973) and associated with reduced copepod growth rates (Twombly and Burns 1996). However, some diatoms in the LSZ may not have been the best food either. Chain-forming diatoms can be poor quality food for copepods that get tangled or have difficulty manipulating long chains (Paffenhoffer 1971; Gliwicz 1980; McNaught et al. 1980; Hartman 1985). This is probably true for the chain-forming diatom, *A. granulata*, that was the most abundant diatom in May. It is not eaten by copepods in Suisun Bay during blooms (Orsi 1995) and is generally only eaten when chain-lengths are short (Fulton 1988).

In addition, the diatom, *Thalassiosira* spp., which was abundant upstream, is poorly assimilated even though it is readily ingested (Ianora and Poulet 1993) and *T. rotula*, which occurred at the center of the LSZ, produces toxins which inhibit copepod egg production and viability (Poulet et al. 1994). Research in other ecosystems suggests diatoms, which comprised most of the optimal sized cells in this estuary, are less utilized and nutritionally inferior to dinoflagellates, whose higher lipid, carbohydrate and protein content are associated with higher egg production and better development in copepods (Kleppel et al. 1991; Ianora and Poulet 1993). Dinoflagellates, however, are not abundant in the Delta (Lehman 1996b).

HISTORICAL PERSPECTIVE

The low chlorophyll *a* concentration, small cell diameter and low diatom density in the LSZ was caused by a number of factors. A long-term decrease in chlorophyll *a* concentration and diatom density throughout the estuary began in the late 1970s (Lehman and Smith 1971; Lehman 1992, 1996a,b). The loss of diatoms probably contributed to the decrease in average cell diameter and phytoplankton biomass, because diatoms are the most abundant large diameter cells in the estuary and have a large cell biomass (Lehman 1996a). These changes in the phytoplankton community biomass and composition were probably caused by a combination of natural and anthropogenic factors and so far have been linked with climate change and water diversions in the estuary (Lehman and Smith 1991; Jassby and Powell 1994; Lehman 1996a,1997). Chlorophyll *a* concentration in the LSZ also decreased by a factor of 10 after establishment of the clam *P. amurensis* in 1987 (Nichols et al. 1990; Alpine and Cloern 1992). This clam may contribute to the loss of diatoms at the center and seaward edge of the LSZ,

because it successfully filters cells >5 μm diameter (Werner and Hollibaugh 1992).

Changes in phytoplankton biomass, community composition and cell diameter in the LSZ may be important to the long-term health of the estuary, because they affect copepod food quality and quantity. Although the diet of copepods in this estuary is poorly known, changes in the quantity and quality of phytoplankton food may have contributed to some of the long-term shifts in copepod species composition and distribution. Densities of many large copepods have decreased (Orsi et al. 1983; Orsi and Mecum 1986, 1996; Obrebski et al. 1992) and densities of many introduced species have increased (Orsi et al. 1983; Orsi and Walter 1991) since the early 1970s. These changes in the copepod community may partially be due to the decrease of phytoplankton cell diameter and biomass in the LSZ (this study) and biomass and diatom density throughout the estuary (Lehman and Smith 1991; Lehman 1992, 1996a,b). The increase in green algae and flagellate species density and biomass over this time (Lehman and Smith 1991; Lehman 1996a,b) may not have compensated for the loss of diatoms, because diatoms are still the most abundant phytoplankton in copepod guts (Orsi 1995).

Shifts in phytoplankton community composition would be important in the LSZ, where the native copepod *E. affinis* was historically abundant (Orsi and Mecum 1986). Research suggests the decrease of *E. affinis* in the LSZ after introduction of *P. amurensis* in 1987 was by direct loss to clam filtration (Kimmerer et al. 1994; Kimmerer and Orsi 1996). This study suggests clams may also have contributed to the shifts in copepod species composition in the LSZ after 1986 by reducing phytoplankton cell diameter and chlorophyll *a* threshold levels to below optimum values.

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